## THE STATUS OF THE MUTATION THEORY, WITH ESPECIAL REFERENCE TO ŒNOTHERA[1]

### DR. HARLEY HARRIS BARTLETT

THE more or less controversial literature of the mutation theory is so scattered and involved that few except specialists have been able to follow it with any degree of satisfaction. A recent book by Gates, "The Mutation Factor in Evolution, with Particular Reference to *Œnothera*," will help the general biologist to an understanding of the situation, but even in the short time since it went to press there have been developments of such significance that I am glad of this chance to review the subject.

The crux of the whole controversy is this: Are the discontinuous variations which occur in cultures of Œnothera true mutations, which might appear either in pure lines or in hybrids, or are they segregates from genetically impure lines? The mutationist and his Mendelian critic give diametrically opposite answers to this question. Some geneticists are beginning to feel that there is justification for taking a middle ground, that the mutations are non-Mendelian, but that they are nevertheless a phenomenon of hybridism, and occur only in impure lines.

The most extensive researches upon mutability have been carried out with *Œnothera Lamarckiana*. This

[1] Papers from the Department of Botany of the University of Michigan, No. 150. Read before the American Society of Naturalists at Columbus, Ohio, 30 Dec., 1915. Based in part upon unpublished experiments conducted at the U. S. Bureau of Plant Industry and published with the permission of the Secretary of Agriculture.

plant gives rise to mutations of two main types, those in
which the chromosome number differs from that of the
parent form, and those in which it does not. The most
striking ones belong to the former category; among them
we need mention particularly only Œ. *gigas* and Œ. *lata*,
which have, respectively, 28 and 15 chromosomes, instead
of 14, the normal number in the species. Gates has espe-
cially emphasized the fact that in the mutating Œnotheras
the pairing of the chromosomes, previous to the reduc-
tion division, is very loose, a condition that would favor
irregularities in the distribution of the chromosomes to
the gametes. By irregular reduction divisions, gametes
with a greater or less number of chromosomes than 7
might easily be formed. From these irregular gametes
there would be derived, in turn, zygotes with irregular
chromosome numbers. Mutationists are now pretty well
agreed that the characters of certain mutations are corre-
lated with an unusual complement of chromosomes. If
one believes at all that the chromosomes provide the
mechanism of Mendelian inheritance, it is hard to escape
the conclusion that the cytological studies of Lutz, Gates
and others give a firm basis for removing at least part of
the mutation phenomena from the domain of Mendelian
segregation.

    Even Davis, who has been one of the chief opponents of
the mutation theory, has admitted that some of the vari-
ants from *Œnothera Lamarckiana* and other species are
probably due to irregularities in chromosome distribu-
tion. He makes the point, to be sure, that the unpaired
condition of the chromosomes previous to reduction in
*Œ. Lamarckiana* is itself exceptional, and presumably the
result of a hybrid constitution. Davis himself has shown
that in at least one of the numerous strains of *Œ. grandi-
flora* which occur at the type locality of that species in
Alabama, the chromosomes, in preparation for the reduc-
tion division, become associated definitely and closely into
ring-shaped pairs. Moreover, this same strain shows a
negligibly low pollen and seed sterility. Davis views it as
essentially a genetically pure strain, whether judged by

its morphology or by its physiological behavior. In 1912 de Vries and the speaker visited the locality from which Davis's strains came, and found such a confusion of different types growing together that it was impossible to doubt that the entire Œnothera population was hybridized to a greater or less degree. Some of the forms belonged to the series of *Œ. grandiflora,* being large-flowered and open-pollinating, whereas others were small-flowered, self-pollinating types, showing obviously the effects of hybridization with *Œ. Tracyi,* another southern species. It is curious that the particular *Œnothera* to be put forward as probably genetically pure, judged by Davis's cytological criterion, or by Jeffrey's pollen test, should come from a locality where hybridization is so prevalent that one would hardly expect to find among the open-pollinating forms a single unhybridized plant. It will be remembered that Jeffrey has attacked the mutation theory from the point of view that pollen abortion necessarily indicates hybridity. By this criterion the small-flowered practically cleistogamous species which self-pollinate generation after generation must be adjudged highly impure, although the evidence is all to the contrary. There is every indication that pollen abortion is a frequent concomitant of mutation, as well as of hybridization. It seems not unlikely, therefore, that the unpaired condition of the meiotic chromosomes may have a causal relationship with pollen abortion as well as with the production of those types of mutations which have a chromosome number different from that of the parent species.

It is ordinarily supposed that a mutation is determined when the reduction division takes place. This may be the case with the mutations in which there are irregular chromosome numbers. Even in such cases it may be that the germ plasm has undergone at some other point in the life cycle a premutative modification of such a nature as really to predetermine the kinds of mutated gametes which will subsequently appear. A physiological premutation might, for instance, bring about the condition which results directly in loose chromosome pairing, and

indirectly in the formation of several different types of mutated gametes. Many mutations are not concerned with such obvious changes as the shifting of chromosomes, but seem rather to depend upon physico-chemical and chemical alterations of the germ plasm. Obviously some such alterations would result in physiological as well as morphological mutations. Just as certain morphological changes are not advantageous, or even distinctly harmful, so certain physiological changes might be harmful and lead to sterility. Some premutations (and by a premutation I mean the inauguration of an unstable condition in the germ plasm) might be of such a nature that the nutrition of the spore mother cells would be interfered with. These might fail to develop, fail to undergo the reduction division or might give rise to defective daughter cells.

Thus mutation, equally as well as hybridization, may account for sterility. There are several groups of plants in which sterility has apparently come about without the possibility of hybridization. Perhaps Davis's genetically pure *Œnothera grandiflora,* with perfect pollen, provides a case of hybridization without subsequent mutability. Those who assert that germinal instability comes about only by hybridization can bring forward no proof of their assertion. Conversely, the mutationist can not prove that any plant in existence has had an unmixed ancestry. The most that he can do at present is to show that mutation takes place in strains which are genetically pure, and that the purity is of relatively long standing. One can only conclude that Davis's and Jeffrey's suggested cytological and morphological evidences of hybridity, if verified, will merely substitute hybridization for premutation as a cause of germinal instability. They will not in any way afford support to the Mendelian conception of mutation.

Nothing could be more obvious than the paths which are marked out for the student of the *Œnothera* problem by the interesting cytological clue afforded by the unpaired chromosomes of *Œnothera Lamarckiana* and other

species. Some one must find out whether or not the unpaired condition occurs in hybrids whose parents do not show it. Strange as it may seem, after all the discussion of hybridity as a possible cause of mutability, no one has yet shown, or tried to show, that mutability occurs in any hybrid between non-mutable parent species. This would seem to be one of the most crucial experiments that could be performed, and one of the easiest. It would be a very attractive problem to attempt to produce the unpaired chromosome condition by hybridization and then to prove it definitely correlated with the particular types of mutability which are characterized by disturbances of the chromosome mechanism.

Even if it were possible in the time at my disposal to review the evidence that the chromosomes provide the mechanism of inheritance, it would hardly be necessary to do so. The brilliant work of Morgan and his students on the association in *Drosophila* of groups of characters with definite chromosomes is well known to every one. In *Œnothera* the investigations of Gates, Lutz and others have shown a connection between chromosome alterations and the characters of certain mutations so obvious that it can not reasonably be disregarded.

There are still a few geneticists, however, who believe that the chromosome cycle has no fundamental significance in connection with Mendelian phenomena. Heribert-Nilsson would ascribe as much weight to a change from flat to crinkled leaves, to choose an example at random, as he would to a change from the 2x to the 4x chromosome number. Such an attitude is forced upon one who attempts to explain all mutations as Mendelian segregates, as this author does. He has made much of a case, observed by Geerts and Stomps, in which the chromosome number of a hybrid between *Œnothera gigas* and *Œ. Lamarckiana* became reduced from 21 to 14, probably through the agency of an irregular reduction division, without the loss of the *gigas* characters. This case is cited to prove that the characters of this mutation do not depend upon the supernumerary chromosomes. Nothing

is more probable, however, than that the chromosomes are qualitatively different, and that the *gigas* characters depend upon the duplication of some, not all, of the chromosomes. An irregular reduction division might well result in the retention in duplicate of those particular chromosomes upon which the *gigas* characters depend. The very characteristic aspect of *Œnothera lata* has been ascribed to its single supernumerary chromosome. Miss Lutz has shown that many mutations with 15 chromosomes do not have at all the characteristic *lata* appearance, which must therefore be attributed to the duplication of a particular chromosome, rather than of any chromosome.

The production of mutations with irregular chromosome numbers is not confined to *Œnothera Lamarckiana.* Two other species have given rise to mutations with 28 *chromosomes,* and in one case, that of *Œ. stenomeres,* the *gigas* mutation is entirely comparable in its characters with *Œ. gigas* de Vries. Its wood structure has been compared with that of the parent species and has been found to present deviations as great as those which are apparent in the external aspects of the two plants. The differences concern not only the relative size of the elements, but also their shape, and, to a certain extent, their distribution. In typical *Œ. stenomeres* the medullary rays are sometimes 140 cells high, whereas in mutation *gigas* they are typically less than 25 cells high, and as far as we have observed, never over 50. It is very significant indeed that striking structural alterations in the most conservative tissues of a plant may be instituted by a single mutative evolutionary step.

As far as the mutations with modified chromosome numbers are concerned, there is the best of evidence that the processes of mutation and Mendelian segregation are absolutely distinct and independent. The evidence is not only cytological, but also genetical, for no mutations of this class show Mendelian inheritance when crossed with their parent forms. Their significance in evolution is illustrated by many widely separated groups of plants in

which species or genera are set apart from their allies by the possession of a different number of chromosomes. Such variations in chromosome number have been found in many cases among the Rosaceæ, a family noteworthy for the complications which it presents to the systematist.   Certain Japanese species of Viola exhibit variations in chromosome number which give a clue to the way in which the numerous forms of this complex genus have evolved.   Similar variations occur among the Orchidaceæ, one of the largest families of flowering plants.

There remain to be considered a large number of mutations in which the chromosome complement has not been shown to differ from that of the parent form.   Such mutations are frequent in *Œnothera*.   De Vries has observed them in the case of *Œ. Lamarckiana* and more recently he and other workers have observed them in other species, belonging to the small-flowered, self-pollinating portion of the genus.   In connection with these mutations it will be necessary to consider more in detail the criticisms brought against the mutation theory by Bateson, Davis, Heribert-Nilsson and others.

In the past, most objections to the mutation theory have been based upon the supposition that *Œnothera Lamarckiana* is a hybrid of garden origin.   I am forced to admit that I am not satisfied with any evidence thus far offered that this species, in the form familiar in cultivation, is or ever was a wild constituent of our flora.   Nevertheless I venture to predict that it will eventually come to light in some obscure locality and that its character as a natural species will be established.   Whether it is a natural species or a product of floriculture is of relatively little importance, however, in view of the fact that none of the mutation phenomena are peculiar to it.   Several other species are known which are equally mutable and which are now elements of our flora.   Moreover, they are small-flowered, self-pollinating forms, and therefore better suited to mutation studies than large-flowered, open-pollinating forms such as *Œ. Lamarckiana,* which in nature must frequently be hybridized.

Before mutation studies had been extended to other species of the genus from Œ. *Lamarckiana,* Davis began a series of experiments with the object of reproducing the latter species as a hybrid of known origin. His first experiments, involving Œ. *grandiflora* as one parent, were unsuccessful in producing a plant that bore more than a superficial resemblance to Œ. *Lamarckiana.* Some of the hybrids showed mutability, but none were obtained which did not show obvious segregation in addition to the mutability. Moreover, the mutations were not shown to have been induced by hybridization, since none of the parent strains were tested for constancy. As de Vries suggested, the mutability was probably an inherited tendency from one or both parents.

Later hybrids, between Œ. *franciscana* and Œ. *biennis,* were much more successful, in that they bore a much closer resemblance to Œ. *Lamarckiana.* The writer saw hybrids last summer in Davis's garden that would surely have been placed by any except the most ultra-critical systematist under Œ. *Lamarckiana.* They are being carried into another generation, and the results will be looked forward to with much interest. A true synthetic Œ. *Lamarckiana* must show mutability, but must otherwise come true from generation to generation. Moreover, it must give twin hybrids in certain crosses with other species. Even if Davis's later hybrids fulfill these conditions, they will not demonstrate the origin of mutability through hybridization, for one of the parents, Œ. *biennis,* has been shown by de Vries and Stomps to be a mutable species, and the other, Œ. *franciscana,* has not been tested. To have much weight, an experiment such as Davis's must show the origin of mutability *de novo* in a hybrid from non-mutable parents.

A more recent phase of the effort to prove Œ. *Lamarckiana* a hybrid dates from the publication, in 1914, of a paper by O. Renner. This author proposed a simple Mendelian hypothesis to account for the twin hybrids and high seed sterility of Œ. *Lamarckiana.* It is well known that in this species about half of the seeds are empty or

do not contain normal embryos. Moreover, when crossed
with certain species, the first hybrid generation consists
of two types, the twin hybrids of de Vries. Renner as-
sumes that Œ. *Lamarckiana* is heterozygous and that it
produces two types of functional gametes. Its progeny
under ordinary circumstances would therefore be ex-
pected to consist of recessive homozygotes, heterozygotes,
and dominant homozygotes in the familiar $1:2:1$ ratio.
He further assumes, however, that the homozygotes are
incapable of developing beyond a young embryonic stage,
and that the species is therefore maintained in a hetero-
zygous condition from generation to generation. This
simple hypothesis obviously does not account for the
mutability of Œ. *Lamarckiana*. It has been amplified
with this end in view by Heribert-Nilsson, whose highly
involved explanation of mutability from the standpoint
of the plural factor hypothesis must receive a brief con-
sideration. For several years this worker has busied
himself in an attempt to demonstrate Mendelian inheri-
tance in Œ. *Lamarckiana*. In one case he thought he had
found simple monohybrid segregation in crosses between
red- and white-nerved races, and announced that the
nerve color acted as a simple Mendelian character. It
developed later, however, that his ratios were aberrant,
and that the progenies entirely lacked a class of plants
homozygous with regard to the supposed dominant char-
acter. According to Heribert-Nilsson's interpretation,
the progenies consisted only of heterozygotes and reces-
sive homozygotes. The elimination of the hypothetical
dominant homozygotes he accounted for by assuming that
in certain cases an incompatibility, or, as he puts it, a
prohibition, exists between like gametes. His whole hy-
pothesis is based upon this idea of prohibition. He as-
sumes that the assemblage of characters which we recog-
nize in *Œnothera Lamarckiana* may be brought about by
many combinations of plural factors. Any one of these
plural factors in the heterozygous condition gives a plant
the *Lamarckiana* habit, and prohibition prevents the pres-
ence of any of them in the homozygous condition. Segre-

gation may lead to the production of pure recessives, lacking all the plural factors which give the *Lamarckiana* aspect. These recessives are the supposed mutations. Pure dominants, on the contrary, can not be realized.

This, in brief, is the Mendelian explanation of mutability. It involves the important assumption that the mutations which breed true are Mendelian recessives. The mutations with irregular chromosome numbers have been shown not to belong in this category. The remaining mutations, for many of which the cytological data are lacking, may conveniently be divided into two classes, (1) those which come true when self-pollinated, or, at any rate, do not include the parent species in their progeny, and (2) those which give a mixed progeny consisting of the mutational and parental forms. If there is any possibility whatever that the Mendelian explanation of mutability is true, it should at least account for the first and simplest of these two cases. We shall therefore confine our attention for the moment to mutations which give a constant progeny.

De Vries found that certain of the original mutations from *Œnothera Lamarckiana* were of the Mendelian type. These mutations are assumed by Heribert-Nilsson to be recessives which have corresponding homozygous dominants, the latter being the strains of *Œ. Lamarckiana* which do not give rise in every generation to the mutations in question. Other mutations, isolated by Heribert-Nilsson himself from *Œ. Lamarckiana,* are produced in every generation, and are therefore, according to this author, recessives which have no corresponding homozygous dominants. If this were the case, they would be recessive when crossed with *Œ. Lamarckiana* regardless of which way the cross was made. As a matter of fact, Heribert-Nilsson made his crosses with *Œnothera Lamarckiana* as the pistillate parent, and therefore obtained the results which he expected. If the crosses had been made the other way, there is very good reason to believe that he would have got the most unexpected results, and would never have advanced his Mendelian hypothesis.

The speaker has recently observed, in several species of *Œnothera* other than *Œ. Lamarckiana,* the origin of a large number of different mutations. Several of these have been found to belong to the type which we are at present considering. That is to say, they give a progeny which does not contain the parent species, and the mutations themselves are produced by the parent species in every generation. In the case of one mutation, described a year ago as *Œ. pratincola* mut. *nummularia,* the chromosome number has been determined as 14, the typical number in the group. The remarkable fact about these mutations of *Œ. pratincola,* as far as work with them has gone, is that their crosses with the parent species are identical with the pistillate parent in the first hybrid generation. Mutation pollinated with parent species yields the mutation. Species pollinated with mutation yields the species.

This most interesting state of affairs is absolutely at variance with the attempted Méndelian explanation. It can be understood on the supposition that two types of gametes are produced, which are by no means equivalent. One type bears most of the characters which differentiate the different species and forms from one another. The other type seems to carry characters which are likely to be common to a number of different species. In the particular species which gives rise to the mutations under discussion the gametes of the former class are female, those of the latter, male. Thus it follows that a mutative modification of the germ plasm in one of these species might affect only characters which were borne by one of the two kinds of gametes. If so, we would have at once a simple explanation of the behavior of the mutations which give matroclinic crosses with their parent species.

The same idea may readily be extended to cover the cases of mutations which give progenies containing both the mutational and the specific types. Perhaps the mutative change is a reversible one, and certain gametes in each generation show reversion from the mutated to the unmutated condition. Or perhaps in some species there

are male and female gametes of both types, but certain
mutative changes are sex limited. In the following dis-
cussion I shall designate the two types of gametes as $\alpha$
and $\beta$ gametes. The former are those which bear the
most distinctive specific characters of the various forms,
whereas the latter bear the more general characters. The
known facts seem to be accounted for if we assume that in
fertilization the conjugation of an $\alpha$ with a $\beta$ gamete ordi-
narily takes place, but not the conjugation of two $\beta$ gam-
etes. In certain cases it seems that fertilization takes
place by the fusion of two $\alpha$ gametes and it appears likely,
also, that some species produce no $\beta$ gametes. Some spe-
cies produce $\alpha$ and $\beta$ gametes of both sexes. Others do
not seem to do so. It sometimes seems to be the case that
the female gametes are all $\alpha$. When a mutation takes
place the modified character is perhaps Mendelian if it is
borne by both $\alpha$ and $\beta$ gametes, but non-Mendelian if it
affects only the $\alpha$ gametes of a species in which fertiliza-
tion takes place by the fusion of an $\alpha$ with a $\beta$ gamete.

This conception of non-equivalent gametes has been
highly developed by de Vries, in a somewhat different way
from that outlined above. It has many obvious advan-
tages in explaining the *Œnothera* situation. It explains
seed sterility as well if not better than the Mendelian
hypotheses of Renner and of Heribert-Nilsson, hypotheses
which are based of course upon the idea of gametic equiv-
alence. It explains why certain reciprocal crosses are
alike, and others unlike, why some of them breed true,
whereas others show segregation, why certain crosses
yield twin hybrids, and why the twins are, respectively,
matroclinic and patroclinic. It also explains other com-
plications which are quite unintelligible from a Mendelian
standpoint. I would by no means give the impression that
there are not many phenomena which remain obscure, but
I do wish to emphasize very strongly that a flood of light
is thrown upon the *Œnothera* situation by the conception
of non-equivalent gametes.

By way of illustration, let us consider for a few mo-
ments the phenomenon which I have called mass mutation.

Mass mutation differs from ordinary mutation only in
that the mutations, instead of being produced in small
numbers, are produced in very large numbers. For ex-
ample, the frequency of mutations in *Œ. Lamarckiana,*
which shows ordinary mutability, is roughly 2 per cent.
In certain strains of *Œ. Reynoldsii* and *Œ. pratincola,* on
the contrary, the number of mutations rises to 50 per
cent., or even 100 per cent., of the progenies. According
to Mendelian conceptions, it is impossible to get extracted
recessives in a progeny in excess of $33\frac{1}{3}$ per cent., and in
order to get this many we must grant the elimination by
prohibition of the corresponding dominants. What shall
we say, then, of progenies containing 499 mutations out
of 500 plants, a condition which has actually been realized
in my cultures of *Œ. pratincola?* It is impossible to in-
voke the elimination of a large class of typical plants, for
the typical zygotes are known to be stronger and better
fitted to develop than the mutational zygotes. My own
explanation is that most of the female germ cells of *Œ.
pratincola* are $\alpha$ gametes and the male, $\beta$ gametes. The
phenomenon of mass mutation consists in the wholesale
production of modified $\alpha$ gametes, $\alpha'$, $\alpha''$, $\alpha'''$, $\alpha''''$, etc., each
of which corresponds to a different mutation and has
characters which impress a distinctive habit on the zygote
which is formed by fusion with an unmodified $\beta$ gamete.
In accord with this hypothesis the reciprocal crosses be-
tween mutation and parent species are matroclinic. Mu-
tation pollinated with species gives mutation. Species
pollinated with mutation gives species.

Mention has already been made of the mutations which
by self-pollination give progenies containing both the mu-
tational and the specific types. If the mutation is cross-
pollinated with pollen from the specific type, the progeny
is a mixture of two types, just the same as if self-pollina-
tion had occurred. On the contrary, if the specific type
is pollinated by the mutation, only the specific type
occurs in the progeny. Here, it seems, we have a case
where the modification which results in the production of
$\alpha'$ instead of $\alpha$ gametes is reversible. Cases of this kind

Heribert-Nilsson refers to (I give a literal translation) as ''heterogamous combinations which are recessive only in the female gametes, but in the male gametes continuously heterozygous.'' As far as I can interpret this vague statement at all, it involves a decidedly unique conception, namely, that the individual $2x$ mutation embodies two different kinds of germ plasm, a homozygous female germ-plasm which will give one kind of cells when the reduction division takes place, and a heterozygous male germ-plasm, which will give two kinds of cells. I think that no one will be inclined to adopt this altogether revolutionary and useless hypothesis. It is by no means certain, after all, that the mutations which show the type of inheritance in question do not belong to the class with irregular chromosome numbers. With one exception they have not been examined cytologically. *Œnothera lata,* a mutation which shows this type of inheritance, has 15 chromosomes. Consequently there is an opportunity for the formation of two kinds of gametes, with 7 and 8 chromosomes, respectively. The male gametes with 8 chromosomes appear to be eliminated. As a result, zygotes are formed with $7 + 7 = 14$ and $8 + 7 = 15$ chromosomes. The former are *Œ. Lamarckiana,* the latter are *Œ. lata.* This beautiful correlation of cytology with inheritance has been worked out by Gates and Thomas.

In either event, whether the mutations which throw the specific type in every generation have a regular or an irregular chromosome number, the mutation hypothesis provides a far more plausible explanation for their behavior than the Mendelian hypothesis.

It must be clear by this time that the speaker finds incredible the arguments that have been brought forward in favor of the idea that mutation and Mendelian segregation are the same. Doubtless it often happens that a mutated germ cell fuses with a typical germ cell and produces an ordinary Mendelian heterozygote. If the mutated character is recessive, and the dominance is complete, the first hybrid generation will of course resemble the parental type, and the second hybrid generation will

show simple segregation. The mutation will appear for the first time in 25 per cent. of the progeny. De Vries has recently reported that the dwarf mutation from Œnothera gigas is of the simple recessive Mendelian type. We must believe, in a case of this kind, that the factor whose modification results in dwarfness is present in all gametes. It does not follow, however, that the gametes are all equivalent with respect to the factors for other characters.

In connection with the discussion of Davis's hybrids which resembled Œnothera Lamarckiana I mentioned that the mutability shown by them was probably inherited from one or both parents. There seems to be some scepticism about the inheritance of mutability as a character. Much of my own experimental work of the last two years has involved Œ. pratincola, a mutable species which has already been refered to several times. There is another species from the same locality which is rather closely allied to Œ. pratincola, but differs in enough regards so that the hybrids between them can be studied with great satisfaction. The second species, Œ. numismatica, is immutable, as far as my experience extends. At any rate it is very much less mutable than Œ. pratincola. The cross Œ. pratincola × Œ. numismatica gives twin hybrids, one of which is exactly like the pistillate parent except in one minor pubescence character. The reciprocal cross, Œ. numismatica × Œ. pratincola, is to all outward appearances the same as the pistillate parent. We have here a most striking case of matroclinic reciprocal hybrids. I am inclined to believe that most of the differences between the two species reside in the $\alpha$ gametes and that the $\beta$ gametes are essentially similar. In accord with this hypothesis nothing could be more interesting than to find that the pratincola-like hybrid is mutable, and produces the same types of mutations that Œ. pratincola itself does. This result, it seems to me, is of the highest significance. It indicates that the germ plasm of Œ. pratincola is in a labile condition, and that this condition is not modified when a zygote is formed by the fusion of its $\alpha$ gamete with the $\beta$ gamete of a different and stable, or at least relatively

stable, species. We could hardly find better proof that such mutations in *Œnothera* involve the $\alpha$ gametes, and are apparent in the zygotes without the need of subsequent segregation because the factors involved have no counterparts in the $\beta$ gametes.

The same crosses, however, afford evidence that certain characters are carried by both $\alpha$ and $\beta$ gametes, and may therefore prove to show Mendelian segregation. The buds of *Œ. numismatica* have a short viscid pubescence which is lacking in *Œ. pratincola*. The matroclinic hybrid *Œ. pratincola* × *Œ. numismatica* can be distinguished from the pistillate parent only by the presence of this hair-type, inherited from the pollen parent. When the second hybrid generation is grown, segregation with regard to this character takes place, and part of the progeny can not possibly be distinguished from *Œ. pratincola*.

In these results we have a clue to the segregation shown in certain hybrids, and the lack of it in others. Most of de Vries's hybrids have involved *Œ. Lamarckiana,* a species, according to my interpretation, with very dissimilar $\alpha$ and $\beta$ gametes. He has therefore obtained and described many measurably constant hybrids. Davis, however, studying *Œ. grandiflora,* which may conceivably have but one type of gametes, has found segregation the rule rather than the exception. In his later studies, involving *Œ. franciscana* and *Œ. biennis,* he has obtained twin hybrids within each of which there was a considerable degree of segregation. All of these varying results will eventually become coordinated as we become more used to distinguishing between non-Mendelian and Mendelian characters.

Another point which must be mentioned is the frequence with which the various types of mutations give rise to one another. For example, two mutations of *Œ. pratincola,* mut. *nitida* and mut. *fallax,* each give rise to plants of mut. *numularia,* which are as typical as though they had been derived directly from *Œ. pratincola*. As already brought out, some mutations appear to be reversible in that they revert to the parent species in part

of every progeny. The germ plasm seems to be a system capable of existing in several different states of equilibrium. Some of these equilibria may be thought of as stable, others as metastable, others as labile, to borrow terms from the physicist. The germ plasm of different species may undergo parallel transformations, resulting in parallel variations. All who have dealt with the species of large genera know that oftentimes the same series of variations turns up in one collective species after another. Many characters have arisen independently, at so many points in different lines of descent, that they have no phylogenetic significance whatever.

It seems to the speaker that the *Œnothera* situation is clearing up. More and more evidence is accumulating which shows that although the phenomena are complex, they are orderly. Probably no two of the workers on the *Œnothera* problem look at it from the same point of view. In this paper I have not hesitated to state freely my present working hypotheses. Next year they may have changed, to fit new facts. Even now there are data at hand which do not accord with the best hypotheses I have been able to formulate, but neither do they accord with any others. Under the circumstances, one should not draw conclusions of too sweeping a nature. It may confidently be stated, however, that the appearance of mutations in *Œnothera* is not due to Mendelian segregation, and that the Mendelian method of attack has been utterly fruitless. It is freely admitted that the mutation processes themselves are hardly understood at all, and that further work must decide whether or not mutation is always or ever conditioned by previous hybridization.

Bateson has recently described the genetical behavior of the rogues which occur in certain varieties of peas. Although he does not suggest that these strange forms are mutations, his evidence would tend to convince a mutationist that they are. Would it not be a strange turn of fate if Bateson, the leader of the Mendelian school and critic of de Vries, were destined to discover mutations of a non-Mendelian type in the very genus which provided Mendel with the material for his classical researches?